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Review

Flavonoids and Strigolactones in Root Exudates as Signals in Symbiotic and Pathogenic Plant-Fungus Interactions

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Abstract: Secondary plant compounds are important signals in several symbiotic and pathogenic plant-microbe interactions. The present review is limited to two groups of secondary plant compounds, flavonoids and strigolactones, which have been reported in root exudates. Data on flavonoids as signaling compounds are available from several symbiotic and pathogenic plant-microbe interactions, whereas only recently initial data on the role of strigolactones as plant signals in the arbuscular mycorrhizal symbiosis have been reported. Data from other plant-microbe interactions and strigolactones are not available yet. In the present article we are focusing on flavonoids in plant-fungal interactions such as the arbuscular mycorrhizal (AM) association and the signaling between different *Fusarium* species and plants. Moreover the role of strigolactones in the

AM association is discussed and new data on the effect of strigolactones on fungi, apart from arbuscular mycorrhizal fungi (AMF), are provided.

Keywords: Arbuscular mycorrhiza, flavonoids, *Fusarium*, root exudates, strigolactones, *striga*, *orobanche*, signaling.

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1. Introduction

Plant roots release a wide range of compounds which are involved in complex communication processes in the rhizosphere. These compounds include sugars, polysaccharides, amino acids, aliphatic acids, aromatic acids, fatty acids, sterols, phenolics, enzymes, vitamins, plant growth regulators and other secondary metabolites [1,2,3]. Although a multitude of soilborne fungi are known to respond to root exudates, an identification of all plant derived signals is still missing. There is no doubt that sugars and amino acids are potential fungal stimuli [4], however, our knowledge on secondary metabolites, which trigger microbe responses in the rhizosphere, is relatively limited [5,6].

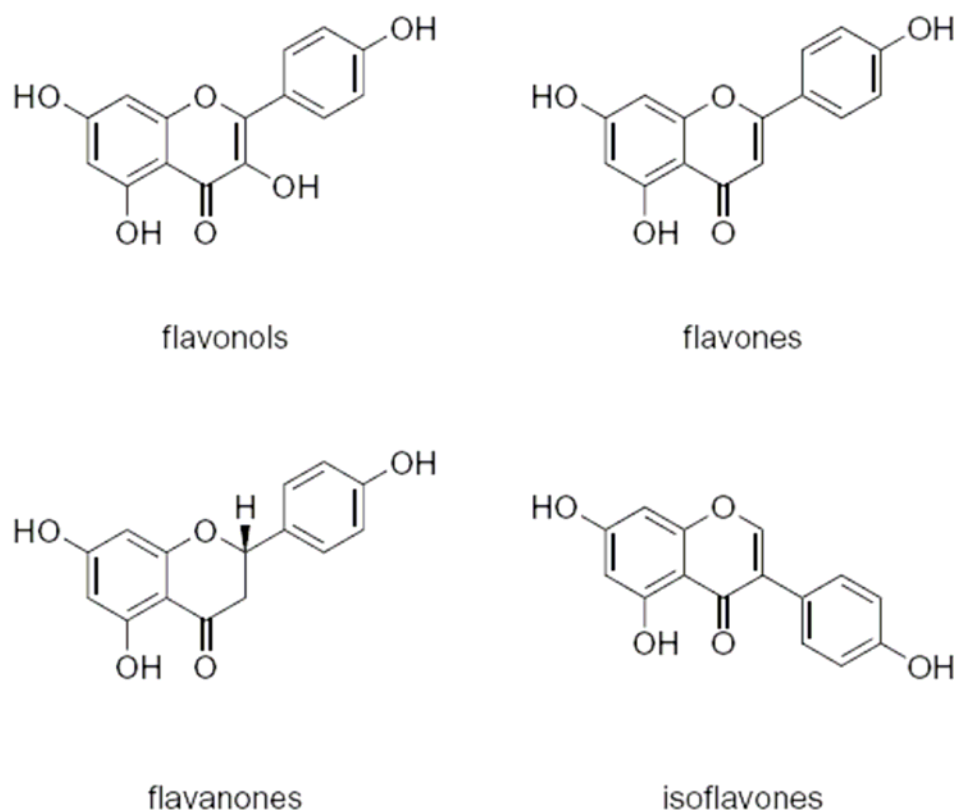
In the present review we focus on two groups of secondary compounds in root exudates which have been reported as key signaling molecules for plant microbe interactions in the soil. Flavonoids are known from a number of plant (primarily legumes) interactions with microbes such as nitrogen fixing rhizobium, arbuscular mycorrhizal fungi, *Fusarium* sp. as signaling compounds and strigolactones, known so far as germination inducers of seeds of the parasitic plants *Striga* and *Orobanche*, very recently have been suggested to play a key role during the establishment of the AM symbiosis. The involvement in signaling of these two compound groups in the symbiotic arbuscular mycorrhizal fungi-plant and in pathogenic fungi-plant interactions is discussed.

2. Flavonoids

Apart from other compounds in root exudates, flavonoids (Figure 1) are known as key signaling compounds in a number of plant-microbe interactions e.g. in the symbiotic *rhizobium*-legume interaction. Flavonoids act as chemoattractants for rhizobial bacteria and as specific inducers of rhizobial nodulation genes (*nod*-genes), which are involved in the synthesis of lipo-

chitooligosaccharide signals, called Nod factors (reviewed in [7]). In roots of legumes Nod factors induce the accumulation of flavonoids resulting in the secretion of more flavonoids by the root, which further stimulate the production of Nod factors by the bacteria [8-11]. Apart from their function in the *rhizobium*-legume interaction, flavonoids also act as signaling compounds in the AM symbiosis and in different plant-soil pathogen interactions.

Figure 1. Chemical structures of the different groups of flavonoid compounds.



2.1. Flavonoids and AMF

Similar to the rhizobium-legume interaction in the AMF - host interaction, root exudates play an important role at the beginning of a signal exchange chain between the host plant and the AMF. As flavonoids are present in root exudates, their involvement in the signaling of the host plant-AMF interaction has been suggested. Abundant data are available on the effect of flavonoids on hyphal growth, hyphal differentiation and root colonization (for more detailed information see reviews [12,13]. A number of flavonoids exhibit a clear stimulatory effect on AMF hyphal growth and this effect seems to depend on the chemical structure of the compound [14-16]. Interestingly the stimulatory effect of the flavonoids has been shown to be even more pronounced in presence of CO₂ at concentrations similar to those found in the rhizosphere [14,15,17]. In most recent studies it has been reported that during pre-symbiotic growth and when applied to plants inoculated with AMF, flavonoids exhibit an AMF fungal genus- and species specific effect [18-20].

Once plants are colonized by AMF the pattern of flavonoids is dramatically changed (see reviews [12, 13]). Interestingly, similar to the effect of flavonoids on different pre-symbiotic stages of AMF [18–20], the alterations of the flavonoid pattern in roots produced by different AMFs also exhibit a certain AMF fungal genus- and species specificity [21,22]. Larose *et al.* [22] and Harrison and Dixon [23] linked the alterations of the flavonoid pattern in mycorrhizal roots to the developmental stage of the AM symbiosis. Whereas during root penetration and the early establishment of AMF intermediate levels of a number of flavonoids are detected in roots, at a later stage of root colonization characterized among others by abundant collapsed arbuscules, high levels of flavonoids such as the phytoalexin medicarpin have been reported [22]. Interestingly the levels of some flavonoids are not only altered in mycorrhizal roots but also in non-mycorrhizal roots of a mycorrhizal plant indicating a systemic regulation of the flavonoid accumulation [24].

To summarize, as different flavonoids can be found in different plant groups, their roles as general signaling compounds during the establishment of the AM symbiosis are questionable [25], however, there are several indications that at a later stage of the AM association; when the AMF is well established, changes of the flavonoid pattern play a regulatory role [22, 24]. Only recently, potential general AM signaling compounds at the pre-symbiotic stage of the AM interaction have been identified in root exudates (see “Strigolactones”).

2.2. Flavonoids and pathogenic fungi

Responses of soilborne pathogens to flavonoids are primarily known for the fungal like oomycetes, such as chemotaxis by motile zoospores of *Phytophthora sojae* [26–28]. These organisms show physiological and morphological similarities to fungi but are phylogenetically different [29]. Apart from this there is only limited information available about flavonoids as signaling compounds for fungal pathogens of legumes [30, 31]. Informations about possible effects of flavonoids in root exudates on root infecting/colonizing fungi of non-legume plants, however, are scarce.

As shown by Ruan *et al.* [30] various flavonoids which occur in root exudates of legumes exhibit a strong stimulatory effect on the macroconidia germination of the pea and bean pathogen *Fusarium solani*. Testing *F. solani* f.sp. *pisi* (pea pathogen) and f.sp. *phaseoli* (bean pathogen) they found highly stimulatory flavonoids. Ruan *et al.* [30] found, that inhibitors of cAMP-dependent protein kinase suppressed flavonoid responsive germination, while nutrient responsive germination was not affected. Thus, they hypothesized, that flavonoids present in root exudates of legumes stimulated the germination of fungi by a different mechanism than those of nutrients. A study of Bagga and Straney [31] reinforced the hypothesis that the macroconidia germination of *F. solani* seems to utilize the cAMP signaling pathway.

Interestingly, Ruan *et al.* [30] found no flavonoid-responsive macroconidia germination for *F. acuminatum*, a pathogen on gramineous plants, and *F. solani* pathogenic on cucurbits. Steinkellner *et al.* [32] tested the effect of 12 flavonoids, representing different classes of flavonoids, on microconidia germination of *F. oxysporum* f.sp. *lycopersici* (*Fol*), the pathogen causing tomato wilt. Applying the flavonoids at five different concentrations, they found no significant effect microconidia germination. In contrast to these authors [30], who found that flavonoids provide a certain level of host specific

recognition among *F. solani* pathogenic on legumes, according to Steinkellner *et al.* [32] flavonoids seems not to be specific stimulating compounds to *F. oxysporum* pathogenic on tomato.

Comparing the germination activity of *F. solani* f.sp. *pisi* in root exudates, Straney *et al.* [33] found the highest macroconidia germination in pea exudates and a partial stimulation in bean exudates, whereas soybean and non-legume exudates did not display a stimulating activity. This effect seems to be host specific and linked with the presence or absence of flavonoids in the specific root exudates as known so far, especially as the germination activity did not correlate with the nutrient level. This specificity to root exudates of the host apparently is no general characteristic for other *Fusarium* species. Investigating the highly specific tomato pathogen *Fol*, Steinkellner *et al.* [34] recently found that not only tomato root exudates but also root exudates of *Fol*-non-host plants, such as sweet pepper, bean, barley, tobacco and cucumber, stimulated microconidia germination. These results suggest that *Fol* germination-stimulating-signals not only occur in root exudates of the host tomato but are general signals in root exudates [34].

Another function of flavonoids on fungal root pathogens has been documented for *F. oxysporum* f. sp. *dianthi*. Interestingly, Curir *et al.* [35] isolated a kaempferide triglycoside in carnation stems and roots, involved in resistance of carnation to *F. oxysporum* f. sp. *dianthi*. There is evidence to suggest that this flavonol functions as typical phytoalexin, responsive to *F. oxysporum* pathogenic to carnation [36].

3. Strigolactones

Striga and *Orobanche* are weeds which can parasitize a number of important crop plants and drastically lower yields. Strigolactones (Figure 2), a group of sesquiterpene lactones, are exuded by roots and stimulate seed germination of *Striga* and *Orobanche* and are present in root exudates in extremely low concentrations [37]. These *Striga* and *Orobanche* seed stimulating compounds are highly instable and have been detected not only in root exudates of host plants for these parasitic plants, but also in root exudates of non-host plants from different plant families (see Table 1).

Figure 2. Chemical structure of the synthetic strigolactone analogue GR24.

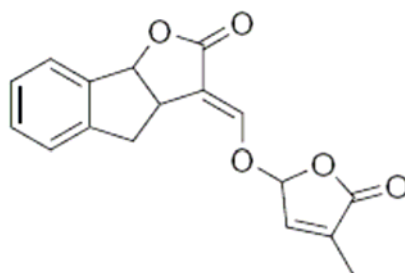


Table 1. Overview on plants where information is available on the presence of strigolactones in root exudates ⁽¹⁾, on the presence of compounds in root exudates exhibiting a stimulatory effect on seed germination of *Striga/ Orobanch* ⁽²⁾ and on the presence of compounds in root exudates stimulating hyphal branching of AMF ⁽³⁾.

Family	Plant species	Host for <i>Striga</i> and/or <i>Orobanch</i>	Strigolact. detected in root exudates ⁽¹⁾	Root exudates stimulate <i>Striga/ Orob.</i> germinat. ⁽²⁾	Root exudat. initiate branching of AMF ⁽³⁾	Reference
Alliaceae	Onion			Orob.		2) [38]
Apiaceae	Celery			Orob.		2) [39]
Asteraceae	Lettuce	<i>Orobanch</i>		Orob.		2) [39,97]
	Sunflower	<i>Orobanch</i>		Orob.		2) [38,39]
Brassicaceae	<i>Arabidopsis thaliana</i>	AM nonhost		Orob.	no	2) [40,41] 3) [42]
	Rapeseed	AM nonhost		Orob.	no	2) [43] 3) [42]
	Cabbage	AM nonhost		Orob.	no	2) [44] 3) [42]
Chenopodiaceae	Sugar beet	AM nonhost			no	3) [42,45]
Cucurbitaceae	Cucumber			Orob.		2) [38,39]
Gramineae	Maize	<i>Striga</i>	Yes	Strig.+Orob.	Yes	1) [46] 2) [38,39,47] 3) [42]
	Sorghum	<i>Striga</i>	Yes	Strig.* +Orob	Yes	1) [46-48] 2) [47, 49*] 3) [42,50]
	Millet	<i>Striga</i>	Yes	Orob.		1) [46, 47] 2) [47]
	Barley			Strig.+Orob.		2) [39,51]
	Oat			Orob.		2) [39]
	Wheat			Orob.		2) [39]
	Ryegrass			Orob.		2) [39]
Lamiaceae	Basil			Orob.		2) [38]
Leguminosae	Pea	<i>Orobanch</i>		Orob.	Yes	2) [53] 3) [42]
	<i>Medicago truncatula</i>			Orob.	Yes	2) [54] 3) [42]
	Alfalfa			Orob.	Yes	2) [39] 3) [42]
	Red clover	<i>Orobanch</i>	Yes	Orob.		1) [55,56] 2) [39]

Table 1. Cont.

Leguminosae	Cowpea	<i>Striga</i>	Yes	Strig.		1) [57] 2) [58]
	Soybean		Yes	Strig.+Orob.		1) [59] 2) [38,60,61]
	<i>Lotus japonicus</i>		Yes			1) [59]
Linaceae	Flax			Orob.		2) [39]
Malvaceae	Cotton		Yes	Strig.+Orob.		1) [56,62] 2) [56]
Solanaceae	Tobacco	<i>Striga/ Orobancha</i>	Yes	Strig.+Orob.	Yes	2) [41,63] 3) [42]
	Tomato	<i>Orobancha</i>	Yes	Orob.	Yes	1) [64] 2) [38,39,65] 3) [42,45]
Tropaeolaceae	<i>Tropaelum majus</i>			Orob.		2) [39]

(1) (2) (3) Blanks in columns indicate no available information

(2) Indication of only one plant indicate no available information for the other plant

*reduced activity when from mycorrhizal plants;

3.1. Strigolactones and AMF

Apart from affecting hyphal growth, compounds released by host roots have been reported to induce branching of AMF hyphae [66–70]. Hyphal branching of AMF has been suggested as one of the events in host root recognition that precedes successful root colonization [42,45,71], as through the branching response “...the probability of encounter with a site on the root suitable for colonization...” [45] is increased. Active branching signals have been reported from a wide range of AM host plants such as carrot, tobacco, corn, sorghum, pea and tomato (Table 1). Recently, Tamasloukht *et al.* [72] determined the time course of action of the root-exuded branching factor. Application of the branching factor to a hyphae resulted in gene activation in *Gigaspora rosea* after 0.5–1h, in alterations at the physiological level after 1.5–3h, and the beginning of hyphal branching could be observed after 5h.

A hyphal branching effect has been reported for a number of flavonoids [16,18,19,73,74], however, as the flavonoids inducing branching can only be found in a limited number of plants, their role as general signaling compounds for hyphal branching as a pre-requisite for a successful AM root colonization seems questionable.

A number of studies attempted to identify the branching factor in root exudates of AM host plants [42,45,75,76], however, only recently strigolactones have been identified as the AMF hyphal branching factor in root exudates of the AM host plant *Lotus japonicus* [59]. More effects of strigolactones and AMF have been reported on a physiological level. In *Glomus intraradices* and *Glomus claroideum*, spore germination was stimulated in the presence of strigolactones and in *G. rosea* the mitochondrial shape and movement were altered and their density in the fungal cell increased [50]. Akiyama *et al.* [77] hypothesized that strigolactones are not only involved as primary

signals for AMF hyphal branching but also as signals for the reported directional growth of AMF towards roots [78,79], however, no data on this effect are available yet.

As strigolactones are present in the exudates of plants from diverse taxa (see Table 1) it has been proposed that they are general essential signaling compounds for the establishment of the AM symbiosis [77]. This hypothesis has been strengthened in a recent paper by Gomez-Roldan and co-workers [80]. They started from the hypothesis of Matusova *et al.* [52] that strigolactones are derived from the carotenoid pathway. Thus, provided that strigolactones are essential signals for the establishment of the AM association, alterations of the carotenoid metabolism could affect the AMF-plant interaction. This hypothesis was tested with maize mutants with a defect in the carotenoid pathway and with maize plants treated with an inhibitor of the carotenoid pathway. In both treatments root colonization by *G. rosea* was reduced, indicating that the levels of important signaling compounds were reduced. Most interestingly, the application of the strigolactone analogue GR24 to the inoculated mutant and inhibitor-treated plants restored the AM root colonization to similar levels as in the control plants [80].

However, these results give rise to a new question. Is the recovery of the AM root colonization in these maize plants after GR24 application due to a stimulation of the AMF spore germination or due to an enhanced branching? It has been reported before that strigolactones stimulate spore germination of AMF [50], thus, in the above mentioned experiment enhanced spore germination could be responsible for the recovery of AM root colonization.

The restored AM root colonization also could be due to the effect of GR24 on hyphal branching. Hyphal branching of AMF has been reported in the vicinity of roots of host plants and has been suggested as an important step that precedes successful root colonization [66-70]. Application of GR24 to the growth substrate of plants as reported by Gomez-Roldan *et al.* [80] should result in profuse branching of the AMF hyphae in the substrate independent of the presence or absence of roots. This could mean that branching by itself is an important step in the AM-plant interaction, but that branching does not have to occur close to the roots of a host plant.

Recent data also suggest a role of strigolactones at a later stage of the AMF-plant interaction, when the fungus is already established in the root. In several studies it has been demonstrated that once plants are mycorrhizal, further root colonization by AMF is reduced compared to colonization of non-mycorrhizal plants [24,81-86]. Looking at these observations it is tempting to speculate that due to altered levels of strigolactones in root exudates of mycorrhizal plants further root colonization by AMF is affected.

In several studies it has been reported that the attachment and the emergence of *Striga* is reduced in mycorrhizal sorghum and maize [49,86-89] and Matusova *et al.* [52] hypothesized that mycorrhization might alter the level of strigolactones and thus affect the seed-germination of parasitic plants through a down-regulation of the mycorrhizal branching factor formation. Data obtained on the effect of root exudates from mycorrhizal and non-mycorrhizal plants on *Striga* seed germination and AMF branching strengthen this hypothesis. Root exudates of mycorrhizal sorghum and maize induced a lower *Striga* seed germination than root exudates of the non-mycorrhizal control plants [49,90] and root exudates of mycorrhizal cucumber plants induced a lower *in vitro* branching of an AMF than exudates of non-mycorrhizal cucumber plants [91,92].

The hypothesis of branching factor(s) in root exudates as a regulating mechanism for root colonization is strengthened further when looking at the effect of root exudates from plants with high P-levels on hyphal branching. It has been reported that at high P-levels in roots the strigolactone production is reduced [93,94]. Hyphal branching in the presence of root exudates from low P-plants has been reported [42,45,75,76]. Interestingly, when root exudates were collected from high P-plants a stimulating effect on branching could not be observed [42,45]. These data indicate that in plants already colonized by AMF or in plants with high P-levels a reduced root colonization is possibly linked with reduced levels of strigolactone in root exudates.

Strigolactones present in root exudates and inducing hyphal branching of AMF have been suggested as important plant recognitions signals for AMF [50,59,77,80]. However, some data on the effect of root exudates on *Orobanch* seed germination and AMF hyphal branching due to the presence of strigolactones in root exudates still seem contradictory. *Arabidopsis thaliana*, rape and cabbage (Brassicaceae) and sugar beet (Chenopodiaceae) are known to be AM non-host plants [96]. Interestingly none of the root exudates of these plants (Table 1; [42,45]) showed a hyphal branching activity on AMF indicating the absence of a branching factor in these exudates, however, root exudates of *Arabidopsis thaliana*, rape and cabbage stimulated the germination of *Orobanch* seeds [40,41,43,44]. Comparing the stimulatory effect of root exudates of carrot, tobacco and *A. thaliana* on *Orobanch* seeds, Westwood [41] reported a reduced level of seed stimulating compounds in root exudates of *A. thaliana*. In our context this could mean that hyphal branching is less sensitive to strigolactones than germination of parasitic weeds of the Orobanchaceae and the Scrophulariaceae. Another explanation could be that specific seed stimulants are secreted by plants of the Brassicaceae which do not exhibit a hyphal branching activity on AMF.

3.2. Strigolactones, *Fusarium* sp. and other fungi

Strigolactones have been reported to be present in the root exudates of a wide range of different plants (see Table 1), thus it would not be surprising that these compounds do not only act as signals for AMF but also for other fungi (e.g. soilborne fungi). To our knowledge no data have been available yet on the effect of strigolactones on other fungi apart from AMF. We tested the effect of the strigolactone analogue GR24, which is known to induce hyphal branching of AMF [59], on fungi from four different groups (Table 2): ectomycorrhizal fungi, beneficial fungi such as *Trichoderma* and *Piriformospora indica*, soil-borne pathogens and the two shoot pathogens *Botrytis cinerea* and *Cladosporium* sp.. With none of the tested fungi any alterations of the branching pattern due to the application of GR24 could be observed.

Moreover, we tested the effect of strigolactones on the microconidia germination of *Fol*. Most recently, it has been reported that strigolactones stimulate the spore germination of AMF [50]; however, we found that they do not affect the microconidia germination of *Fol* (Steinkellner and Mammerler unpublished results). These preliminary data indicate that strigolactones are specific signals for AMF but not general plant signals for fungi. However, further studies are needed to confirm this hypothesis.

Table 2. Effect of the strigolactone analogue GR24 on hyphal branching of different fungi.

Fungal group	Fungus	Growth medium	Observation after treatment	Effect on branching
Ectomycorrhiza	<i>Paxillus involutus</i>	½ modified Melin Norkans medium	22, 24h	No
	<i>Laccaria bicolor</i>	½ modified Melin Norkans medium	22h	No
	<i>Amanita muscaria</i>	½ modified Melin Norkans medium	22h	No
	<i>Cenococcum geophilum</i>	½ modified Melin Norkans medium	16h	No
Beneficial fungi	<i>Trichoderma</i>	Water agar	16h	No
	<i>Piriformospora indica</i>	Nutrient agar	18h	No
Soil-borne pathogen	<i>Rhizoctonia solani</i>	Water agar Potato dextrose agar	6 , 16, 40 h	No
	<i>Fusarium oxysporum</i>	Water agar Potato dextrose agar	16, 38h	No
	<i>Verticillium dahliae</i>	Water agar Potato dextrose agar	23h	No
Pathogen on aerial plant parts	<i>Botrytis cinerea</i>	Water agar	23h	No
	<i>Cladosporium sp.</i>	Water agar	6, 30h	No

Experimental set-up: About 1.5-2 mm in front of the colony growing in a petri dish small holes (approx. 2 mm diam.) were punched with a plastic pipette and the content was removed by suction. To the holes H₂O or GR24 (which had been diluted in acetone), or the same acetone concentration as in the GR24 treatment (12 µL) were applied (for further details see Nagahashi and Douds [45]). Before observation with a microscope, a lactophenol cotton blue solution was sprayed onto the mycelium in the petri dish to obtain a better contrast. To assure the use of an active GR24 solution, the GR24 solution (0.1 mg/L which was before diluted in 0.1 mL acetone) was tested on the germination of *Striga hermonthica* seeds before. Growth conditions of fungi: All tested fungi were grown in the dark at 24 °C. *Piriformospora indica* was kindly provided by Katarzyna Turnau/ Kraków/Poland.

4. Conclusions

Flavonoids in root exudates are known as signaling compounds in a number of pathogenic and symbiotic plant-microbe interactions; however, their importance seems to depend highly on the specific interaction. Whereas these compounds are known as key signals in the rhizobium-legume interaction, despite their effect on AMF spore germination, hyphal growth and differentiation, their effect on AM root colonization and their altered accumulation pattern in mycorrhizal roots, an essential role of flavonoids for the outcome of the AM symbiosis has been questioned [25]. From all the data accumulated on flavonoids and AMF a general role of flavonoids as signals at an early stage of the interaction, during the establishment of the AM association, seems unlikely, however, a

potential role in the regulation of mycorrhization, once the AMF has colonized the host root, can not be excluded.

In several *Fusarium*-plant interactions an effect of flavonoids on micro- and macroconidia germination has been reported, however, nearly no data are available yet on hyphal growth and the role of flavonoids during infection. Moreover, to our knowledge scarce data are available about alterations of flavonoid level in plants infected by *Fusarium*. Thus, further studies are needed to elucidate their exact role in this interaction.

Strigolactones only recently have been identified as important signals in the AMF-plant interaction and thus are “hot issues” in mycorrhizal research. To our knowledge no data are available yet about their implication as signaling compounds in other plant-microbe interactions. Our preliminary data with a number of different fungi indicate that strigolactones are specific signaling compounds for the AMF-plant interaction and are not involved in similar signaling events in other plant-fungus interactions, however, due to their nearly ubiquitous presence in the root exudates of plants it would not make wonder to find the involvement of these compounds in the signaling of other plant interactions. We are convinced that in the near future there will be some new and exciting data in the field of strigolactones and plant interactions.

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